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Authors: McBrayer, Lance D., and Anderson, Roger A.

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Sexual Size Dimorphisms and Bite Force in the Northern Alligator Lizard, *Elgaria coerulea*

LANCE D. McBRAYER^{1,2} AND ROGER A. ANDERSON³

¹Department of Biology, PO Box 8042, Georgia Southern University, Statesboro, Georgia 30460, USA; E-mail: lancemcbrayer@georgiasouthern.edu

³Department of Biology, 516 High Street, Western Washington University, Bellingham Washington 98225, USA

ABSTRACT.—Bite force capacity is a directly related performance correlate of head shape and is an integrative measure of performance in capturing and handling prey, fighting, and mating, especially for males. We investigated head shape and bite force dimorphisms in a small semifossorial lizard (*Elgaria coerulea*) that exhibits females-larger sexual size dimorphism (FL-SSD) in some populations but not in others. Specifically, we explored how body size, head shape, and bite force compare between the sexes relative to any dimorphisms in body or head size in a coastal population of *E. coerulea*. Female larger-SSD was confirmed for this population, but it contrasted with males-larger sexual dimorphism in head size (ML-SDHS). Males also had greater bite force than females of similar size. The secretive habit of *E. coerulea* hampers observations of behavioral interactions among conspecifics. However, it is expected that lizards with FL-SSD will have ML-SDHS if males with greater bite force win fights with other males over access to mates and/or if greater bite force increases copulation success.

In lizards, many taxa are known to exhibit sexual dimorphism in body size (sexual size dimorphism, SSD). Several hypotheses about the causes for SSD have been presented (Vitt and Cooper, 1985; Stamps et al., 1997; Butler et al., 2000; Cox et al., 2003; and references therein). Other influences on body size being equal for both sexes, the “fecundity advantage” hypothesis predicts females-larger SSD (FL-SSD) in lizard species at high latitudes or elevations where activity seasons are short, age at first reproduction is delayed, reproductive seasons are short, and reproductive frequency is low (Fitch, 1981; Cox et al., 2003). In contrast, again with other influences on body size being equal for both sexes, the males-larger SSD (ML-SSD) is expected if males with greater access to mates are those that win in intrasexual competition for mates and those that win are larger (1) in body size, (2) body robustness, (3) in some feature that enhances combat, such as size of the jaw-cranial complex, or (4) in all three features (as seen in *Aspidoscelis tigris*; Anderson and Vitt, 1990). Even among males of similar body length, the winners of male combat may be those with greater body robustness and head size (Herrel et al., 2001b, 2005; Lappin et al., 2006b).

Lizards (Squamata: Lacertilia) are a particularly useful taxon for studying the evolutionary ecology of SSD and other sexual dimorphisms because of the great variation within and among

lizard taxa in body size, FL-SSD, ML-SSD, and the sexual dimorphism of other features (Brana, 1996; Stamps et al., 1997; Butler et al., 2000; Cox et al., 2003). In addition, several North American lizard species are known to exhibit variation in SSD among populations (*Sceloporus* [Fitch, 1978]; *Elgaria coerulea* [Stewart, 1985]; *Crotaphytus collaris* [Baird et al., 1997]; *Phrynosoma* spp. [Zamudio, 1998]). Thus, lizards may be a model system to investigate the ecological causes of SSD and any associated trade-offs that result from SSD.

Elgaria coerulea is the northernmost, smaller-bodied species of its genus, and is the only viviparous species in this genus of average sized, secretive, thigmothermic lizards (Stewart 1979, 1985; Fitch 1981; Rutherford, 2004). Females-larger SSD is commonly hypothesized to have a direct relationship to increased fecundity with increased body size in female lizards; hence this relationship and its morphotypic consequences may also occur in *E. coerulea* if it exhibits FL-SSD. Therefore, we investigated whether other features associated with intrasexual selection, such as sexual dimorphism in head size (SDHS) and maximum bite force occurred in a northern, maritime population of *Elgaria coerulea*, despite the expected occurrence of FL-SSD in this population. Bite force is linked to musculoskeletal features of the cranial-jaw complex, such as length, width, and height of the complex (Herrel et al., 2001a,b, 2007; Lappin et al., 2006b). Maximum bite force is a useful performance measure because it may contribute to exclusive access to mates through male-male

²Corresponding Author.

combat, ritualistic copulation bites, and the proficiency in capture and handling of prey (Herrel et al., 1996, 1999, 2005; Verwajen et al., 2002; Lappin and Husak, 2005). Thus if ML-SSD occurs and male bite forces are greater in *E. coerulea*, despite FL-SSD, then we can posit that sexual selection for head size occurs in this secretive lizard.

MATERIALS AND METHODS

Elgaria coerulea were captured on west-facing and south-facing talus slopes and rock-faces interdigitating with forest edge, at 2–20 m elevation between Chuckanut Bay in Whatcom County and Samish Bay in Skagit County, Washington (48.6°N, 122.5°W). Each lizard was toe-clipped for identification, sexed by eversion of hemipenes, weighed, and measured for snout-vent length (SVL). Each lizard was also measured to the nearest 0.1 mm for head length, head width, and head height using Vernier dial calipers. Head length was measured along the midline from the tip of the snout (premaxilla) between the external nares to the posterior aspect of the parietal. Head width was measured at the dorsolateral margin of the quadrate at its articulation with the squamosal. Head height was measured at the anterior margin of the tympanum (quadrate bone) from the parietal to the ventral side of the ramus of the mandible.

Lizards were held in five-gallon glass terraria on a 12 : 12 light : dark cycle at Western Washington University for 2–14 days. Each terrarium contained a small refugium (up-turned plastic dish with 3-cm sides), a warming stone, and water dish. Lizards were maintained on a diet of domestic crickets dusted with vitamins. All animals were cared for in accordance with the National Research Council (1996).

Bite forces were measured with a dual cantilever bite-bar. Each aluminum bar had foil strain gauges bonded to it and measured $30 \times 10 \times 1$ mm (separation = 4 mm). The gauges were configured as a wheatstone bridge circuit so that displacement of the bars resulted in a change in resistance in the circuit. This change in resistance (in millivolts, mV) was digitized and stored on a computer.

The mV output from the bite meter was calibrated by applying masses (0.5, 1.0, 2.0, 4.0 kg) onto the bite bars at 2 mm from the bar tips. By doing so, the relationship between the mV output of the meter and actual forces in newtons was estimated as $\text{newtons} = 0.044X - 0.105$ ($R^2 = 0.97$). Thus, any millivoltage recorded at the 2 mm position could be converted to newtons of bite force.

Lizards were warmed to their preferred body temperature of 30°C (RAA, unpubl. data), then induced to bite. Bite gape at the rubber-covered bite bar tips approximated the head height of adult lizards. The transducer was positioned so that only the anterior premaxillary and dentary teeth bit the transducer at 2 mm. Off-center bites were excluded. Each lizard bit the transducer during 3–5 biting trials and the maximum bite force of these trials retained for statistical analysis.

Because some populations of *E. coerulea* are known to exhibit SSD and other populations do not (Stewart, 1979, 1985), we first tested the hypothesis that this coastal population exhibited SSD. Analysis of variance (ANOVA) was used to test for significant differences in SVL between males and females. This SSD data set included all adult male and female lizards captured at this site in 1998, 2000, and 2001 (recaptures were excluded; $N = 86$). A combination of analyses was used to determine whether lizards differed in head size and bite force. First, we wanted to know whether males and females differed in absolute head size and, thus, used ANOVA to test for differences in head length, head width, and head height. If size differences were observed, then analysis of covariance (ANCOVA) was used to test for relative differences between males and females when scaled to equivalent SVL. The same approach was taken to test for differences in absolute (ANOVA) and relative (ANCOVA) differences in bite force. Testing for relative differences in head size and bite force is important because sexual dimorphic characters can result from simple allometric differences between the sexes (Johnson et al., 2005). The head shape and bite force data sets included the same individual lizards captured in 1998 ($N = 19$; 10 males, 9 females). Prior to statistical analyses, all data were checked to ensure they conformed to the assumptions of ANOVA and ANCOVA.

RESULTS

Pooling SVL data across the three years, we found that females have greater SVL than males (i.e., FL-SSD; ANOVA; $F_{1, 85} = 17.21$, $P = 0.00008$) but were not different from males in head length (ANOVA; $F_{1, 18} = 0.77$, $P = 0.39$) or head width (ANOVA; $F_{1, 18} = 0.03$, $P = 0.87$; Table 1). Males had significantly higher heads than females (ANOVA; $F_{1, 18} = 8.61$, $P = 0.009$). Thus, females in the population are larger than males in absolute body size (SVL), but males still have higher heads.

Because males and females exhibited significant difference in body size, we also tested for

TABLE 1. Descriptive statistics of morphological and performance variation in male and female *Elgaria coerulea*. Cells containing different letters (*a*, *b*) are significantly different (ANOVA). Cells containing different numbers (1, 2) are significantly different after correcting for size differences (ANCOVA). See text for explanation.

Variable	Sample size		Mean \pm SD		Range	
	Male	Female	Male	Female	Male	Female
SVL (mm)	39	47	88.3 \pm 4.78 ^a	92.3 \pm 4.24 ^b	79–96	84–103
Bite force (newtons)	9	10	20.18 \pm 2.9 ^{a1}	15.0 \pm 4.03 ^{b1}	14.4–24.0	9.87–21.5
Head height (mm)	9	10	8.18 \pm 0.46 ^{a1}	7.42 \pm 0.65 ^{b2}	7.3–8.7	6.2–8.3
Head length (mm)	9	10	17.0 \pm 1.03 ¹	16.6 \pm 0.94 ²	15.7–19.0	14.4–17.8
Head width (mm)	9	10	11.1 \pm 0.68	11.0 \pm 1.38	10.1–12.5	9.0–13.4

differences in head shape (i.e., relatively larger or smaller head size when scaled to equivalent body size). Analysis of covariance (covariate = SVL) revealed that males had significantly higher heads than females (head height: slopes: $F_{1,15} = 0.23$, $P = 0.63$; intercepts: $F_{1,16} = 24.72$, $P = 0.0001$; Fig. 1). There also was a trend—albeit not statistically significant—for males to have longer heads (slopes: $F_{1,15} = 0.37$, $P = 0.55$; intercepts: $F_{1,16} = 3.75$, $P = 0.07$), but head width was the same for males and females of similar body size (slopes: $F_{1,15} = 0.005$, $P = 0.95$; intercepts: $F_{1,16} = 0.33$, $P = 0.57$).

Significant differences were observed between sexes in bite force; males had significantly higher absolute bite forces than females (ANOVA; $F_{1,17} = 8.55$, $P = 0.009$) and relative bite forces (ANCOVA (covariate = SVL) slopes: $F_{1,15} = 0.054$, $P = 0.82$; intercepts: $F_{1,16} = 17.56$, $P = 0.0007$; Fig. 2). Males and females of similar head height (however, had similar bite forces (ANCOVA [covariate = head height] slopes: $F_{1,15} = 0.40$, $P = 0.54$; intercepts: $F_{1,16} = 1.55$, $P = 0.23$; Fig. 3).

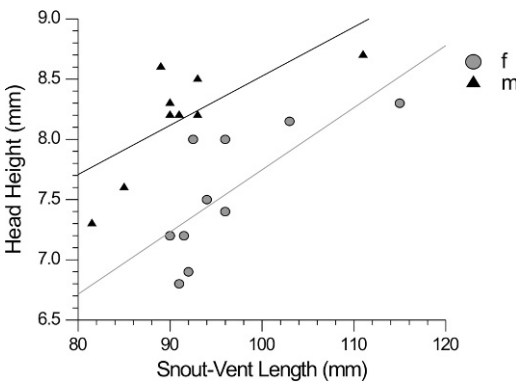


FIG. 1. Sexual dimorphism in head height and body size in *Elgaria coerulea*.

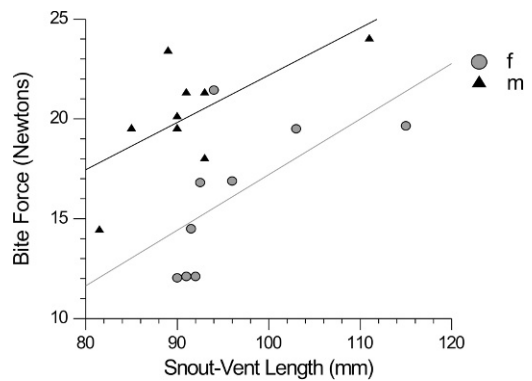


FIG. 2. Sexual dimorphism in bite force in *Elgaria coerulea*. Males bite harder than females even when scaled to similar body size.

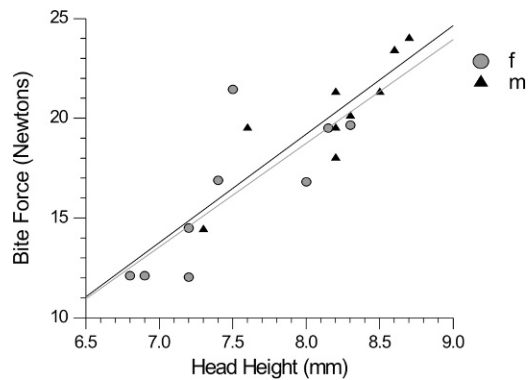


FIG. 3. Relationship between head height and bite force in *Elgaria coerulea*. Although males and females are significantly different in bite force (Fig. 2), this difference is mediated by increases in male head height so that when scaled to equivalent head heights, no sexual dimorphism in bite force is apparent.

DISCUSSION

Like Stewart (1979, 1985) and Rutherford (2004), we found that FL-SSD exists in this coastal Washington population of *E. coerulea*. Head height was the only morphometric variable to show sexual dimorphism with our sample size (Fig. 1). In lizards, male-male combat has been cited as a frequent mechanism by which sexual dimorphism in cranial morphology may arise (Fitch, 1981; Tokarz, 1995; Censky, 1997; Herrel et al., 2001a), and many lizards are known to exhibit an array of sexually selected cranial features (e.g., dewlaps, spines, etc.) that may be related to combat or display (Anderson and Vitt, 1990). Some sexual dimorphisms in cranial features serve as important sexual cues (Cooper and Vitt, 1988; Vanhooydonck et al., 2005) and/or may be related to fighting ability (Lailvaux et al., 2004; Lappin and Husak, 2005; Lappin et al., 2006a). Despite FL-SSD in *E. coerulea*, either the advantages of intrasexual selection (male combat) or intersexual selection (female choice) could be the cause for the observed differences in head morphology and performance. We know of no reports of combat or mate-advertising displays in *E. coerulea*; thus, we do not know whether males vigorously compete for access to mates. Direct behavioral observation of combat, mating, or individual assessment of differential male fitness will be required to test this hypothesis in the future.

Anecdotal observations of a few males with head scars are the only current evidence to suggest that males engage in combat. A reasonable alternative hypothesis to sexual selection for males with relatively larger heads is selection for enlarged cranial jaw complex for food acquisition in males as a means to obviate the disadvantage of smaller asymptotic body size in males. Although similarity between the sexes in diets is typical for lizards (Vitt and Cooper, 1986; Verwaijen et al., 2002), ML-SDHS may be accompanied by larger and harder prey in the diets of adult males (Herrel et al., 1999; 2006), but a thorough dietary analysis will be required to test this hypothesis for *E. coerulea*.

In *E. coerulea*, head height is greater in males, and sexual dimorphism in head height is related to sexual differences in bite force (Fig. 2). Like many lizards, male *E. coerulea* bite females during copulation and may maintain a mouth-grip on females for several hours (Svihla, 1942). Greater head height gives males a better mouth-prehension on the head, neck, or abdomen of larger females (Herrel et al., 2001a,b). Because the sexual differences in bite force disappeared once males and females were scaled to similar head heights (Fig. 3), the

expanded cross-sectional area of jaw muscles caused by greater head height is likely the mechanism of increased force production. Hence, males have the advantage of larger body size (larger heads) without having to actually attain larger bodies (which may be limiting for secretive, crevice-dwelling lizards).

Allometric differences in the ontogeny of head form (height and length) between the sexes results in males having a greater head length per unit size (mm SVL). Thus, males have a greater absolute gape at the tip of the jaws associated with less gape angle because the head is larger. Having greater absolute gape is ecologically relevant to males because (1) they mouth-grip females during mating and (2) combat with other males would be facilitated with a smaller maneuverable body and large head in tight crevices. Given that the jaws act as a simple lever system, the increase in head length alone would decrease the mechanical advantage of the jaw system because the distance over which the applied muscle force acts would increase. Increasing head height, however, compensates for the loss of jaw-tip bite force associated with a forward (prognathic) extension of the jaws. Increasing head height may achieve this in several different ways, for example by shifting the muscle vector forward (i.e., making it straighter) or by allowing more adductor musculature to be packed into the jaw adductor chamber. Thus, a proportionately longer and higher head allows males an effectively greater gape for biting the wide body of the female and yet still provides the force generating capacity to grip the hard, slippery dorsum of the female's trunk.

Increases in head width could also compensate for the loss of bite force at greater head lengths by allowing for more muscle tissue to be packed onto the skull (Herrel et al., 1999; Lappin et al., 2006b). A flatter head (and narrow body), however, may be more of a feature of adaptedness for movement than head width in narrow openings like rock crevices (Herrel et al., 2001b; Lappin et al., 2006b) because head height is always less than head width (Table 1). All *E. coerulea* captured for this study were found under and near large rocks and boulders and at crevice-laden rock faces; the species is known elsewhere to also occur inside rotten logs and stumps and under bark (Fitch, 1935; Stebbins, 1985; RAA pers. obs.). Thus, *E. coerulea* is most frequently associated with living in or near surface structures with cracks and crevices to use as refugia. It is possible that the strong association of *E. coerulea* with narrow openings has influenced the evolution of the gracile, elongate, head-and-body form, including short legs (Anderson, 2007).

Despite the apparent advantage for both sexes to have dorsolaterally compressed heads-and-bodies for living in crevices, the greater head height of *E. coerulea* males than in females is presumably a result of counter-selection. That is, ML-SD in head height is a correlate of greater bite force in males because greater bite force is an advantage in acquiring mates (Lailvaux et al., 2004; Lappin and Husak, 2005). Herrel et al. (2001b) showed a positive relationship between head height and bite force among three closely related species of crevice-dwelling lizards; the species with the greatest head height (*Xenosaurus newmanorum*) had the most powerful bite force and lived in the largest crevices. Furthermore, our results match those of Lappin et al. (2006b), which demonstrate trade-offs in bite force, head length, head width, and head height. These authors show that bite force capacity and variation in head shape are best predicted by head height in another sexually dimorphic, crevice dwelling, lizard (*Sauromalus ater*).

The FL-SSD in this population of *E. coerulea* may support the fecundity advantage hypothesis or the hypothesis of early maturation of male mate searching at the expense of energetics (particularly in populations with high mortality [Cooper and Vitt, 1989; Rutherford, 2004; Cox et al., 2005]). The ML-SD in head height and maximum bite force, however, are a strong basis for hypothesizing the presence of strong sexual selection in this species, despite the FL-SSD. The contrast in FL versus ML dimorphisms provide a mechanistic understanding into the nature of how sexually dimorphic characters evolve and are maintained. Thus, further work, especially detailed investigations on resources use (diet and microhabitat), the ontogeny of head shape, and male-male interactions, is required in species exhibiting FL dimorphisms.

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